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ADDRESS OF THE PRESIDENT FOR 1914.

SOME POINTS IN THE DEVELOPMENT OF THE NOSE.

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No exhaustive treatment of the subject is here attempted. For the most part this article is a review of the literature and attempts to set certain recently discovered facts into relation with older observations on the nose and its development. Whatever may be offered in the way of theoretical conclusions we trust will be of value in pointing the way to a more clear understanding of our problems yet unsolved.

Although Max Schultze showed in 1862 that the adult olfactory nerve arises from cells located in the nasal epithelium many anatomists and embryologists of later date persisted in making it homologous with a typical ganglionated sensory nerve of the body region. Some anatomists looked upon the olfactory bulb as the ganglion. With the advent of the Golgi method and the description of the relation of the mitral cells and their glomeruli to the olfactory tract this idea had to be abandoned. Moreover it was shown embryologically that the olfactory bulbs, so often quite far removed from the brain as in the sharks, develop from the forebrain and are not in any way similar to dorsal root ganglia.

Among those who found a ganglion in the developing olfactory nerve may be mentioned such men as Milnes Marshall, Balfour, von Kölliker, Beard and Chiargui. The idea in the minds of most of these men was that the head nerves are segmental and homologous

with those of the body. These attempts to homologize the cranial with the spinal nerves may be attributed to the trend of zoological thought in the time in which they wrote. The recently accepted evolution theory of Darwin led embryologists to look for evidences of the derivation of the vertebrates from segmented forms like the annelids. On this assumption the cranial nerves, even the olfactory, might be found to have a ganglion in its development. That these men found a ganglion on the olfactory nerve can no longer be doubted.

In all chordates higher than *Amphioxus* the first evidence of the olfactory organ is a thickening of the epithelium of the embryo not far from the closure of the neuropore. Following Kupffer we may designate this the nasal placode. Kupffer found the earliest placode to be single in the Cyclostomes and argued for a primitive monorhinal condition in vertebrates. I think we may agree with Karl Peter that the monorhinal condition that seems to exist in larval Cyclostomes is secondary, on account of their parasitic habits, perhaps. At any rate the olfactory nerves are paired and there are two sets of folds in the Schneiderian membrane of adult Cyclostomes. In other higher vertebrates these placodes are always paired and according to Peter, distinct from each other from the first. He was unable to confirm the finding of an unpaired connection between the two as cited by Gage for a human embryo of 4.3 mm. length. I thought I found an unpaired placode in *Amia*, but the matter needs further investigation to learn whether this unpaired placode is not a cord of cells left from the closure of the neuropore.

In pig and man the first thickening of the ectoderm occurs before the embryo attains a length of 5 mm., and later the depression that deepens into the nasal sac is soon evident. At this time there is considerable thickness of loose connective tissue mesoderm intervening between the nasal placodes and the neural tube. This makes it easy to determine that the olfactory nerve grows inward from the placode and does not originate from the neural tube. In lower forms like some of the fishes, the olfactory placode is in contact with the neural tube when it can first be detected with certainty.

The veteran embryologist, Wm. His, Jr., working on mammalian embryos, was the first to cause the idea that the olfactory nerve

is derived from the ectoderm exclusively, to pass current in the realm of embryology. Also, he found a ganglion, wandering out from the nasal epithelium to produce neuroblasts for the formation of the fila olfactoria as well as the formation of supporting elements. He believed that the true nervous elements of the ganglion pass over to the olfactory bulbs. This would leave an adult olfactory nerve free of ganglion cells in accordance with the adult condition described by Schultze cited above. This origin of the ganglion from the ectoderm through the thickening of the nasal epithelium is in direct contrast with the ideas of Beard and others who sought in the ganglion a homologue of neural crest. Disse is the other noted investigator of the development of the olfactory nerve whose work seems generally accepted by embryological writers today. Working on birds, he confirmed the work of His in finding the ganglion to arise from the olfactory epithelium. He showed that there was never a ganglion of considerable size. By the Golgi process he discovered that there were only a very few true nerve cells. In older embryos these nerve cells were found nearer and nearer to the olfactory bulbs. The majority of the cells migrating from the nasal epithelium were believed to become sheath cells of the fila olfactoria.

Bedford followed up the work of Disse on the birds by similar methods both cytological and neurological applied to the pig. He confirms the findings of His and Disse as to the origin of cells along the fila olfactoria from the nasal epithelium. He says the majority of these cells do not form nerve cells. He mentions the suggestion of Disse that they form supporting cells, but closes by saying he did not determine their fate. In a series of papers undertaken to clear up the embryological history of the nervus terminalis, I have come to the same conclusion as the authors cited above, viz., that a ganglion arises in the course of the olfactory nerve whose cells come from the nasal epithelium. No evidence of origin of any part of this ganglion from the brain or any other source than that named, is at hand.

It is the presence of the nervus terminalis in all groups of vertebrates from sharks to man as shown by a series of papers published during the past decade by various authors that calls for a new examination of the relation of the embryological ganglion on, or near,

the olfactory nerve. The older observations of the ganglion on the olfactory nerve did not take account of the nervus terminalis. The embryological observations undertaken since the discovery of the nervus terminalis have not been in complete accord in regard to the relation of the embryological ganglion to the olfactory nerve and the nervus terminalis. Locy, the discoverer of the nervus terminalis in the sharks, was at first of the opinion that the nervus terminalis has a common origin with the olfactory nerve. Later he came to the view that there is a separate origin for the two and

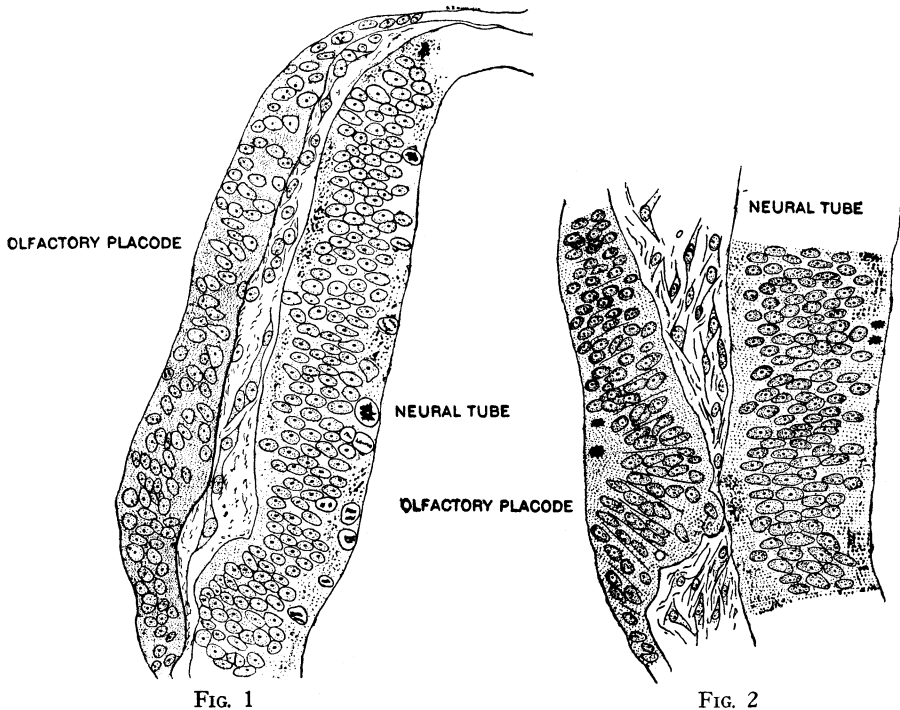


FIG. 1. Section of a transverse series through the olfactory placode of *Chrysemys martinata* nearly 4 mm. long. On account of head flexure the section is approximately horizontal in this region, as are all of the others. X 250.

FIG. 2. Similar section of 4 mm. *Chrysemys* embryo, showing slight advance in development of olfactory placode which is now in contact with the neural tube. X 250.

that the *nervus terminalis* is a separate segmental nerve of a more anterior segment than the olfactory.

Later Belogolowy working on selachians, found both the olfactory nerve and the *nervus terminalis* to be derived from what he designates a primitive olfactory ganglion arising out of the olfactory thickening of the ectoderm. My observations on series of graded embryos of fresh-water fishes as previously published, are in accord with Belogolowy except that I do not see the need or propriety of calling the ganglion a primitive olfactory ganglion. No evidence has presented itself to me that *fila olfactoria* are developed from the ganglion. The evidence is in favor of the origin of olfactory neuraxones from cells that never wander from the Schneiderian membrane of the nasal mucosa.

The following account of the development of the olfactory nerve and the *nervus terminalis* in relation to the ganglion in the turtle, *Chrysemys marginata*, will serve to illustrate the embryological history of the two nerves. The history is the same as that found in the fishes. I am indebted to my former pupil, Mr. Albert B. Myers, for the drawings and help in preparation of the sections.

When the *Chrysemys* embryo measures 4 mm. total length the ectodermal thickening of the nasal placode can be recognized over a wide area in front of the optic vesicles. The nuclei of this epithelium occupy three or four indefinite layers (fig. 1). The thickness is slightly greater in the posterior part of the placode. The section is cut approximately horizontal on account of the head flexure. At the anterior end of the neural tube the ectoderm is in contact with the neural tube, but over the greater part of the extent of the nasal placode scattered mesodermal cells are interposed. The mesodermal cells increase in number and compactness farther ventrally and a small capillary could be detected.

Figure 2 is of a size marked the same as the specimen from which the preceding figure was drawn but shows a slight advance over it. The placode has thickened and come into contact with the neural tube. Adjacent section shows limiting membranes broken down and a slender protoplasmic bridge extending from the placode into the neural tube. The mesodermal elements are more compacted than in the previous stage.

When the embryo has reached a slightly larger size (fig. 3) the nasal epithelium has increased in thickness and number of cells. The basement membrane is wanting over much of its deeper surface and a strand of fibers pierces the neural tube. Adjacent to the strand of fibers can be seen a clump of cells just emerging from the nasal placode. They are slightly larger than the remainder of the placodal cells and show an irregular disturbed arrangement, whereas the placodal cells are disposed in rows perpendicular to

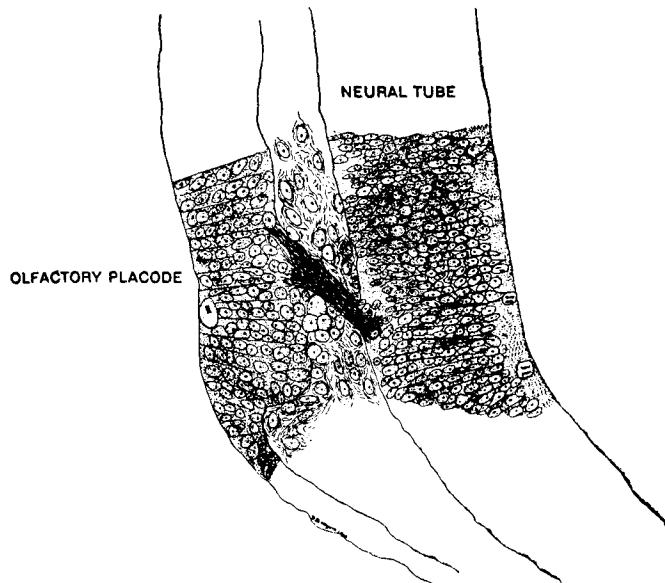


FIG. 3

FIG. 3. Section of *Chrysemys* about four and one-half mm. long. The olfactory nerve fibers are beginning to develop and the cells of the *nervus terminalis* are migrating from the nasal placode. X 250.

the outer surface where the mitotic figures are always plentiful. It is from these emergent cells that the ganglion on the olfactory nerve arises.

In an embryo of the same length as the above, which shows by the nasal pits a degree of advance in development, the olfactory

nerve is shown cut through its entire length (fig. 4). The cells are seen to occupy a position in the nerve and on its lateral border. The cells here shown nearer to the brain tube than the olfactory epithelium, are not the only ones along the nerve, as is evident from other sections.

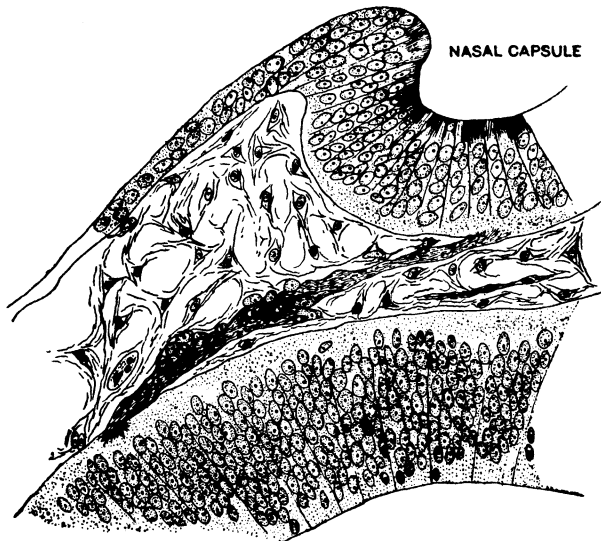


FIG. 4

FIG. 4. *Chrysemys* 5 mm. long with nasal pit forming and a number of cells of the olfactory ganglion intimately associated with the olfactory nerve. X 250.

When the embryo has increased to nearly six mm. length, the size of the olfactory nerve is larger and the number of cells along it is more numerous (fig. 5). The artist has drawn all the cells to appear as neuroblasts with vesicular nuclei. Whether all are of this character is uncertain. The main ganglion is located near the nasal epithelium where the olfactory nerve breaks up into smaller twigs.

We have not followed the development of the ganglion in the turtle through to the *nervus terminalis* of the adult as we did in the fishes, but we have no doubt that such an adult structure exists. Johnston has described the *nervus terminalis* in another turtle,

practically adult. We have followed out the early developmental history in a cyprinoid fish (probably a horned Dace, work still unpublished) and found the evidence the same, viz., that the cells

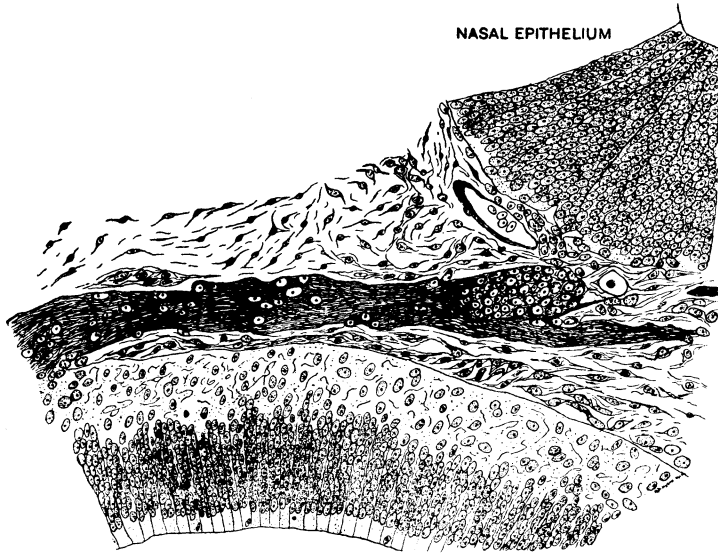


FIG. 5

FIG. 5. *Chrysemys* of nearly 6 mm. length showing the ganglion of the nervus terminalis near the blood vessels at the base of the nasal epithelium. These cells show the characters of neuroblasts. There are other cells scattered along the olfactory nerve as far as its union with the brain. X 250.

along the olfactory nerve arise from the nasal epithelium and that these cells give rise to the nervus terminalis. That some of these cells may give rise to the sheath cells of the olfactory nerve is very probable. As the sheath cells are distributed as far posteriorly as the olfactory bulbs and there is often a ganglion terminale not far from the olfactory bulbs, we readily harmonize our findings with the statements of His and Disse, noted above, that cells from the embryological ganglion pass over to the olfactory bulbs.

DISCUSSION

If other embryological investigations show that the above account of the origin of the nervus terminalis from the olfactory placode is correct, it would seem to me to prove that the nervus terminalis is a component of the olfactory nerve. I have previously taken this view of the matter and Johnston has emphasized it. That the nervus terminalis is not homologous with the nerve to Jacobson's organ is quite clear. The nervus terminalis is present in forms where the vomeronasal organ is absent or rudimentary as in man. Read has shown that Jacobson's organ has nerve fibers of the true osmotic type. Although the nervus terminalis is frequently intimately associated with the ramus to the organ vomeronasale it may exist side by side with the nerve to Jacobson's organ, as Johnston has shown, or be distributed in part to a region anterior to the organ of Jacobson as demonstrated by Huber and Guild. We are in no position to state definitely the relation existing between the organ of Jacobson and the nervus terminalis so long as we are uncertain of the function of either of them. With regard to Jacobson's organ we may incline to the view expressed by Peter that it serves various functions in the different vertebrate classes. It may be glandular in part and it may serve for sex recognition, for testing the expired air, or for recognition of harmful food-stuff in the mouth. If it serves these various functions it may very well be that the structure is not strictly a homologous organ in all the vertebrates where found. Evidently it is not so essential as the nervus terminalis which seems everywhere present in the vertebrates so far as known.

I have been hunting for a type of vertebrate where the nervus terminalis is hypertrophied so as to gain further evidence of its function. No such case has been found. The nerve is developed *pari passu* with the development of the nasal sac. This is in keeping with the function that I have suggested previously, that it is in part an autonomic nerve. The opinion of Huber and Guild is in accord with this view with the reservation that its central connection does not conform to their idea of a typical autonomic nerve. It may be that it contains general somatic sensory fibers as suggested by Johnston. The recent work of McKibben on the sharks by *intra vitam*

methylen blue emphasizes two facts. The cells are not constant in position or grouping and they are not of a type such as we should expect in a typical somatic sensory ganglion. Instead of being T-shaped unipolar cells, or bipolar, they are largely of multipolar variety so far as impregnated in his various preparations. Huber and Guild noted many multipolar cells in the rabbit and they have been conspicuous in the fishes that have come under my observation.

In addition to the common embryological origin of the nervus terminalis and the olfactory nerve noted above is to be mentioned the observation of Pinkus, the discoverer of the nervus terminalis in fishes, that it has the same peripheral distribution (nasal mucous membrane), the same central ending (prosencephalon), and the same nature of supporting (sheath) cells without medullation, as has the olfactory nerve. In general these statements hold true today in light of our extended knowledge. However, there seems to be a central connection with parts of the brain more posterior than the olfactory region of the forebrain. McKibben traced the central path to the interpeduncular region of the mesencephalon, and in *Amia* there is apparently a tract reaching as far as the optic chiasm or farther.

The exclusively placodal origin of the nervus terminalis and the olfactory nerve does not bring the nasal segment into closer correspondence with the other cranial nerves. The homologue of the neural crest which the early workers on the cranial nerves sought does not seem to be present. However, it does seem to emphasize the close relationship between the sense of smell and that of taste. It is quite well known that there is a marked physiological correspondence in the fact that we discriminate between taste and smell with difficulty in many instances. Herrick has discussed their probable origin from a common chemical sense, the olfactory organ into an exteroceptor and the taste-buds into interoceptors. Landacre has shown that epibranchial placodes occur on those nerves only that contain gustatory fibers. Thus it might seem that the sense of smell and the sense of taste originated from cells that were located not in the main axial group included in the neural plate, but from cells scattered in the skin as placodes, primitive sense organs.

When we attempt the comparison of the sense of smell and the sense of taste on the morphological side we meet with some

difficulties. It is true there are arguments that can be adduced to show that the nasal cavities are probably gill slits. The nose is quite commonly intimately connected with the mouth, which is admittedly a gill slit. I have gone so far as to figure a supply of blood to the nose of *Amia* through the internal and external carotid arteries similar to that given to the pseudobranch. The nasal folds in the Schneiderian membrane of fishes can be compared to gill filaments and Blaue went so far as to compare the groups of osmotic cells in some fishes to taste-buds. I have noticed an apparently similar grouping in the nasal cavity of young *Amblystomæ*. But if the structures in the nose sometimes resemble taste-buds, they are not really similar. Gustatory cells are conceded to have very brief basal processes not reaching beyond the taste-bud, while olfactory cells send their axones into the glomeruli of the olfactory bulb and leave the olfactory nerve without a ganglion except the *nervus terminalis*. This is not thought to be large enough to serve the transmission of the sense of smell if it made the proper cranial connections. Thus, the osmotic sense retains that primitive position of its neurones in the integument like invertebrates, as was first pointed out by Retzius, I believe. It may be that an early development of a protective nasal capsule has lessened the necessity for withdrawal of the neurones from the outside. It has occurred to me that the residence of the neurone body in the epithelium where the chemical stimuli are received may add to the delicacy of smell over taste as shown by Parker and Stabler in experiments on each other with dilutions of alcohol.

We may summarize the development of the olfactory nerve by saying that the present evidence points to the embryological as well as morphological distinctness from other nerves. It is more closely allied in its development to taste-bud components of cranial nerves, but its neurones remain in the ectoderm. The development of the *nervus terminalis* along with the olfactory nerve from the same placode is unique among nerves that are somatic sensory or sympathetic.

Little Rock, Arkansas.

February 22, 1915.

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